TRADE-OFFS AND CO-BENEFITS BETWEEN FARMLAND BIODIVERSITY AND ECOSYSTEM SERVICES IN LOWLAND AGRICULTURAL SYSTEMS IN THE UK

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BACKGROUND

A key finding of the UK NEA was that land-use change in the UK over the past 40 years had increased the output of provisioning services, mainly agricultural production, at the expense of a range of regulating and cultural services. The UK NEA went onto show that when the value of some of these other ecosystem services is taken into account, it transforms the way land-use change is viewed (Bateman *et al.*, 2013). UK NEA scenarios in which agricultural output values were highest (National Security and World Markets) actually had the lowest total monetised value when the values of greenhouse gas emissions (GHGs), recreation and urban green space were taken into consideration. Conversely, scenarios with the lowest agricultural output values (Green and Pleasant Land and Nature@Work) had the highest total monetised values due to the value of these ecosystem services.

What are the potential implications of this broader ecosystems perspective for biodiversity? Although the way biodiversity fits into an ecosystem services framework is currently somewhat confused (Mace *et al.*, 2012), there are two contrasting possibilities. Since at a very general level biodiversity is an integral part of the processes that underpin ecosystem services (MEA, 2005; TEEB, 2009; Mace *et al.*, 2012), it is often assumed that protecting ecosystem services would also have biodiversity benefits (Foley *et al.*, 2005). That is, there are co-benefits between biodiversity value and the value of ecosystem services. Alternatively, biodiversity conservationists often express concern that an emphasis on ecosystem services might undermine existing biodiversity conservation priorities (Mace *et al.*, 2012). This would be true if there were a trade-off between biodiversity value and the values of other ecosystem services. These possibilities have yet to be explored in any detail, but the UK NEA data provides an opportunity to do so.

Interestingly, analyses of biodiversity in the UK NEA scenarios suggested that scenarios that had the highest total monetised value might also have the highest biodiversity value, and *vice versa* (Bateman *et al.*, 2013) (see also Fig. 22, p52; *NEA Synthesis of Key Findings*). If true, this would imply that land-use change that reduced GHG emissions and improved recreational and urban green space values might also have biodiversity co-benefits. This could be crucially important for biodiversity conservation in the UK because it would mean that conservation could be a simple by-product of policies and practices that seek to manage land in a way that maximizes value across a range of ecosystem services. This possibility was not explicitly tested; however, within the original NEA. Furthermore, the measure of biodiversity value used (bird species richness, (Bateman *et al.*, 2013)) does not equate with UK conservation priorities, which are typically based upon the population (or range) trends of individual species (Gregory *et al.*, 2004; Gregory and van Strien, 2010). It is unclear,

therefore, whether measures of biodiversity value that better reflect current conservation priorities behave in a similar way to species richness measures used in the original analysis (Bateman *et al.*, 2013).

Our aim here is to explore the relationships between the values of ecosystem services quantified by the UK NEA scenarios and biodiversity values to identify trade-offs and co-benefits between biodiversity and ecosystem services. To do this, we focus on lowland agricultural areas within the UK for two reasons. First, it is in these areas that the intensification of agriculture has led to substantial increases in the output of provisioning services (crop and livestock production) whilst resulting in significant biodiversity loss and ecosystem degradation (Vickery *et al.*, 2001; Robinson and Sutherland, 2002; Foley *et al.*, 2005; Stevens *et al.*, 2010). Second, there is a substantial body of knowledge on the relationship between biodiversity and land-use change that can be used to assess biodiversity value. If co-benefits with other ecosystem services are important, we would expect to see biodiversity value increasing across the UK NEA scenarios as the total value of the other ecosystem services increases. That is, it should be highest for the Green and Pleasant Land and Nature@Work scenarios, and lowest for the National Security and World Markets scenarios. In contrast, if trade-offs with other ecosystem services are important we would expect to see the opposite pattern – biodiversity value should decrease across the UK NEA scenarios as the total value of other ecosystem services increases. The aim of our analysis was to distinguish between these possibilities. Note that we excluded the values of urban green space from our analysis because these are not important in the context of agricultural landscapes.

Although farmland biodiversity consists of a wide range of plant and animal species (Butler *et al.*, 2007; Butler *et al.*, 2009), our analyses focus of farmland birds. This is because a range of modelling approaches exist that allow us to quantify how land-use change is likely to affect the ecological value of farmland for birds (Butler *et al.*, 2010; Butler and Norris, 2013); and the long-term population trends of birds are well characterised in the UK (Fuller *et al.*, 1995; Siriwardena *et al.*, 1998; Fewster *et al.*, 2000; Gregory *et al.*, 2004; Gregory and van Strien, 2010). Such quantitative approaches are simply not feasible for other biodiversity groups at the present time. Specifically, we apply two approaches to the UK NEA scenario data. First, we use functional space models (FSMs) to explore how the land cover/use changes predicted by the UK NEA scenarios might impact on the population trends of the 19 farmland bird species that make up the farmland birds index (FBI) (Butler and Norris, 2013). This approach translates agricultural land-use into the quantity and quality of nesting and feeding resources required by each species, and then explores how this functional space relates to population growth. In this way, it is possible to use FSMs to explore how land-use change is likely to impact on population trends due to the way it modifies the quantity and quality of available nesting and feeding resources. Second, we use a mechanistic model of seed-eating birds to explore how UK NEA land cover/use changes might impact on seed resources and hence on bird species dependent on these resources. This is potentially important because increased annual mortality linked to the loss of seed-rich habitats has been identified as a key demographic mechanism behind the declines of a number of farmland bird species (Siriwardena *et al.*, 2000). Furthermore, increasing the availability of seeds during

winter can improve survival and local abundance for certain species (Peach *et al.*, 2001; Siriwardena *et al.*, 2007). This means that seed-eating species are a sensitive ecological group to land-use change; hence their inclusion in our analyses.

METHODS

Functional Space Models

Our FSMs were originally developed using the land-use classification system adopted by the Breeding Bird Survey (BBS) and Winter Farmland Bird Survey (WFBS) (Butler and Norris, 2013). We used BBS/WFBS land-use data because our original analysis combined this with bird census data collected by BBS to explore how bird population trends relate to functional space. The FSMs translate land cover/use data into the quantity and quality of nest and foraging resources available to each species (functional space), and then describe the relationship between functional space and the annual rate of population growth across all BBS squares occupied by a particular species. We have developed functional space models for all 19 species that make up the farmland birds index (FBI) (Butler and Norris, 2013). Subsequently, we have tested our FSMs to see how well they are able to reconstruct current population trends based on functional space, particularly distinguishing species with a declining trend from those with a stable/increasing trend; and have shown the models are adequate as a basis for quantifying population trends across the 19 species (Helen Hicks *et al* unpublished data). This means we can use the models as a basis for assessing changes in biodiversity value associated with changes in land cover/use.

In order to apply our FSMs to the UK NEA land cover/use data associated with the scenarios we have to translate the UK NEA classification system into BBS/WFBS land-use classes. Since the BBS/WFBS classification system used by our FMSs is finer-scale than the UK NEA system, this requires a set of rules that disaggregate the UK NEA land cover/use classes into the various BBS/WFBS land-use classes within them. We treated the BBS and WFBS data separately because our FSMs use these data to estimate the quality and quantity of functional space available during the breeding (BBS) and non-breeding (WFBS) periods (Butler and Norris, 2013). First, we assigned BBS/WFBS land-use classes to the closest land cover/use classes recognised by the UK NEA. Next, we estimated the areas covered by each BBS/WFBS land-use class within the different UK NEA land cover/use classes. For BBS land-use data, we calculated the number of BBS transect sections covered by each NEA land cover/use type, then converted these into functional space components for each species. To do this, we assumed that the relative proportions of our BBS land-use types within the UK NEA land cover/use classes reflected those in the BBS data. This meant that as land-use changed across the UK NEA scenarios we assumed that the proportions of our BBS land-use types within each UK NEA land cover/use class remained the same. In principle, BBS data can then be used to disaggregate the UK NEA land cover/use classes into the land-use types and associated functional space required by our model on a square-by-square basis. This was not possible in all cases, however, because of discrepancies between the BBS and NEA datasets. To overcome this, we adopted a similar process to that applied below for seed-eating birds.

For WFBS data, we treated non-arable and arable land-use types differently. This is because an arable land-use type may change into a range of different habitats over the winter depending on the rotation system, and these different habitats are likely to have very different ecological values. For non-arable land-use types, we disaggregated UK NEA land cover/use data into WFBS land-use types by first allocating WFBS land-use classes to the land cover/use classes recognised by the NEA; then estimating areas of WFBS land-use types assuming, in a similar way to BBS data, that the proportions within an NEA land cover/use type remained constant across all the NEA scenarios. We used a similar process for dealing with discrepancies between WFBS and NEA data (see below).

For arable land-use types, the areas of NEA arable land-use types (cereal, oil seed rape, root and other) may either remain in production over the winter or enter a fallow period (e.g. stubble) depending on the relative frequency of autumn (remains in production) and spring (fallow/stubble) sown crops. This distinction is ecologically important because stubble habitats provide key food resources for farmland birds over the winter (Gillings *et al.*, 2005). We used DEFRA June Census and HGCA crop management advice to estimate the proportion of autumn and spring sown crops in each NEA arable land-use type. The ratio of autumn to spring sown cereal varies regionally driven mainly by the area of barley. Each 2-digit national grid cell was assigned to a GOR (Government Office Region) and the proportions of autumn and spring sown cereals from DEFRA data were assigned to all 1x1km squares falling within the 2-digit grid cell. There is no evidence that root crops are sown in autumn so we assumed all were spring sown. There are no records of spatial variation in the relative area under autumn or spring sown oil seed rape; overall 95% of oil seed rape is autumn sown so this was applied across all squares and scenarios. Since the NEA arable land-use type 'other' consists of a range of land-uses we simply assumed that the ratio of autumn to spring sown was 50:50. Having separated NEA arable land-use types into crops and fallow/stubbles we then assigned WFBS land-use types to these classes. We estimated the functional space for each species from the WFBS data assuming the relative proportions of each WFBS land-use type remained constant within NEA land-use classes across scenarios. We used the same process to dealing with discrepancies between NEA and WFBS data as outlined below.

In this way we set-up our FSMs for the BASELINE and six UK NEA scenarios and used them to estimate the annual population growth rate for each of the 19 farmland bird species in each scenario. For each species, the model was run for every 1x1 km square in which the species was recorded as present in at least three or more years between 1994 and 2007. From these outputs we could estimate national population trends for each species, and for the farmland bird's index.

Mechanistic Models of Seed-eating birds

Our mechanistic model of seed-eating birds is a spatial depletion model based on a series of patches (fields) within a landscape that vary in the type and quantity of seeds available to seed-eating birds based on crop type and management (Butler *et al.*, 2010). The model tracks the availability of crop (oil and cereal seeds) and weed seeds through the post-harvest

(stubble) period in these fields from summer through the subsequent winter on a daily basis. It incorporates seed mortality in the form of predation by birds and other losses, and seed input due to seed rain (weed seeds). The model can then be used to ask whether food resources are sufficient to support a specified number of seed-eating birds over the winter. This is usually expressed as bird-days (number of birds x number of days) supported over the winter, and hence this statistic provides a measure of the value of a landscape for seed-eating birds. The model recognises two types of seed-eating birds – a yellowhammer-type that preferentially forages on cereal seeds but will also consume weed seeds; and a linnet-type that avoids cereal seeds but forages on oil and weed seeds. This was done to reflect the ecological diversity among seed-eating bird species.

We have previously set-up the model so it can simulate seed dynamics and seed-eating bird populations for over 500 1x1 km lowland agricultural squares covered by the Breeding Bird Survey (BBS) and Winter Farmland Bird Survey (WFBS) (Butler *et al.*, 2010). By changing land-use within these squares according to the UK NEA scenarios we can explore the potential impacts on seed-eating bird populations. To do this we needed to translate the NEA land-use data into the availability of over-winter stubbles arising from the crop types recognised by our model. Firstly, land-use change in the UK NEA was estimated at 2x2km square scale, so the areas of each land cover/use class were divided by four so the data matched the scale required by our model. Next, we assumed that *Cereal* (UK NEA land cover/use class) could represent either Wheat or Barley, *Oilseed* (*UK NEA land cover/use class*) could represent either Oil Seed Rape or Linseed and that *Root Crop* (*UK NEA land cover/use class*) was sugar beet; these are the five stubble types (Wheat, Barley, Oil Seed Rape, Linseed, Sugar Beet) recognized by our model. All other UK NEA land cover/use classes were regarded as unsuitable habitat for seed-eating farmland birds.

The relative proportions and temporal dynamics of different stubble types were originally determined in our model by patterns in existing data on stubble availability derived from WFBS (details in (Butler *et al.*, 2010)). We assumed that the relative proportions of our different stubble types within the UK NEA land cover/use classes reflected those in the WFBS data. This meant that as land-use changed across the UK NEA scenarios we assumed that the proportions of our stubble types within each UK NEA land cover/use class remained the same. For example, the relative areas of wheat and barley stubbles within the UK NEA *Cereal* land-use class remained the same across all NEA scenarios. In principle, WFBS data can then be used to disaggregate the UK NEA land cover/use classes into the stubble-types and associated dynamics required by our model on a square-by-square basis. This was not possible in all cases, however, because of discrepancies between the WFBS and NEA datasets – for certain squares a crop type was present in the UK NEA data but absent in the WFBS data. To overcome this, all WFBS squares were assigned to a 100km square on the basis of their two-letter National Grid code. We then used the relative areas of our stubble types averaged over all WFBS in the 100km square to disaggregate the UK NEA land cover/use classes in 1km squares with these discrepancies. In a few cases, there were even discrepancies between WFBS and NEA data at the 100km square level; the NEA predicted the presence of a particular crop type in certain 1km squares when that crop was not recorded as stubble in any 1x1 km WFBS square within its associated 100km square. In these cases we

averaged WFBS data from adjacent 100km squares.

In our original model, the absolute areas of each stubble type and the way these changed over the winter were determined by WFBS survey data. WFBS recorded the areas of different stubble types during three visits over the winter beginning in November. While we can use WFBS data to disaggregate the UK NEA land cover/use data into the stubble types required by our model (see above), the WFBS only provides relative rather than absolute areas of the different stubble types in this respect. This is because by the time the first WFBS survey is done in November many fields are likely to have re-entered cultivation and are hence unavailable as foraging patches for seed-eating birds. We are unable to estimate this fraction from the UK NEA land cover/data e.g. we are unable to estimate the proportion of the *Cereal* UK NEA land cover/use class that remained a stubble until November. We assumed, therefore, that the entire area of each UK NEA land cover/use class persisted as a stubble until November, after which we used WFBS data to determine the areas of different stubble types, and stubble gains and losses over the winter. This assumption clearly over-estimates the availability of seed-rich habitats for seed-eating birds, but since the same assumption was made across NEA scenarios we are able to compare model outputs between scenarios, and look for spatial associations between model outputs and other ecosystem services within scenarios.

In this way, we set-up our model for the BASELINE and six UK NEA scenarios using the land cover/use data generated by these. We populated each square with 500 individuals of each bird ecotype (i.e. 'yellowhammer' and 'linnet'). This density was considered high enough to allow discrimination between landscapes in terms of resource availability and population persistence without being so high that resource availability was insufficient for populations to persist (Butler *et al.*, 2010). Note that this bird density is higher than we used previously (Butler *et al.*, 2010) but reflects the fact that we over-estimate seed availability (see previous paragraph). All other parameters, such as initial seed densities, levels of weed seed rain and seed survival were similar to those used previously (Butler *et al.*, 2010). We ran the model for each UK NEA scenario and extracted the total number of bird-days supported over the winter for each square as a measure of its ecological value for seed-eating birds.

RESULTS

Model testing

To check whether our translation of the UK NEA land cover/use data into the land-use data required by our models, we conducted two model tests. First, we would expect the population
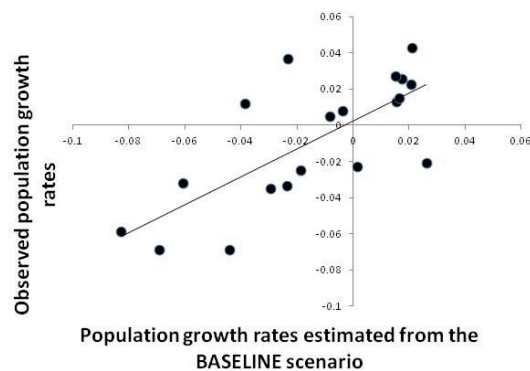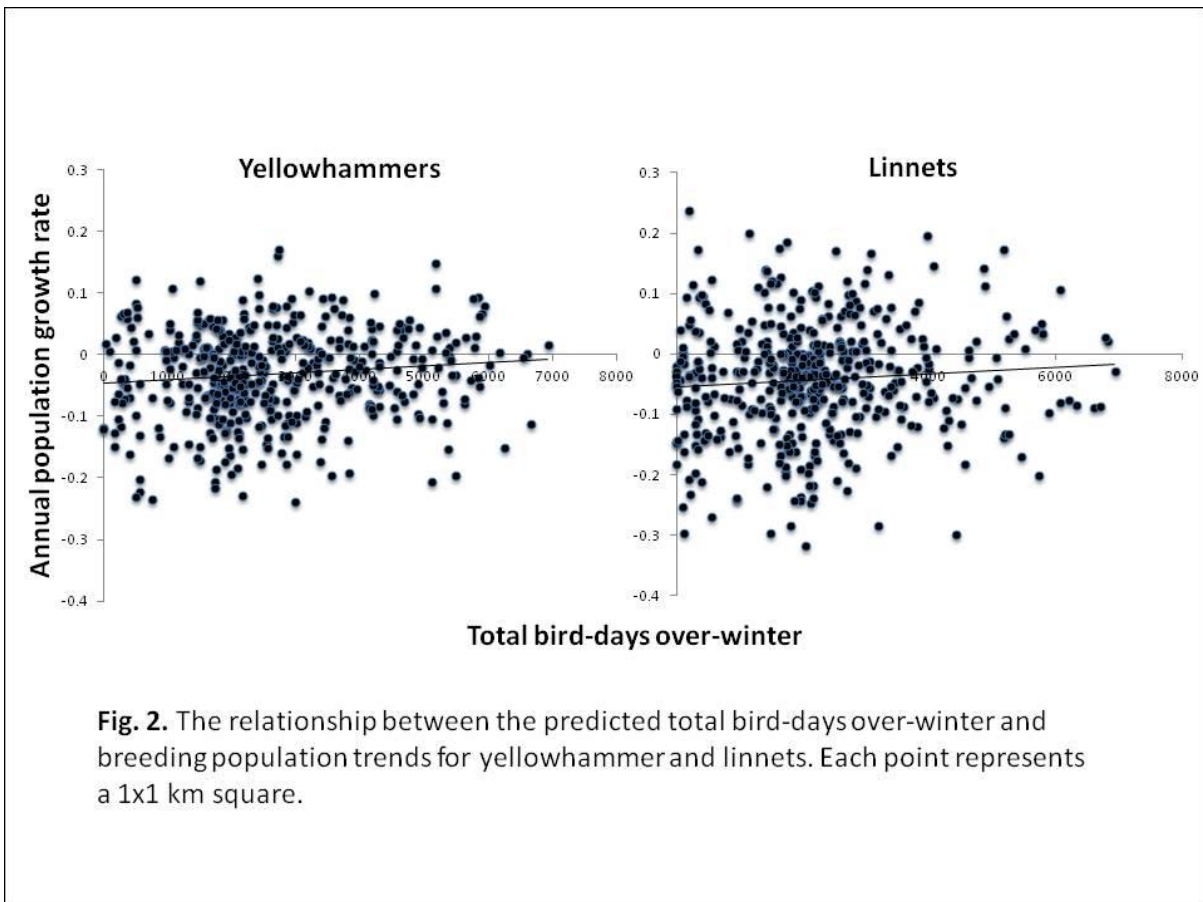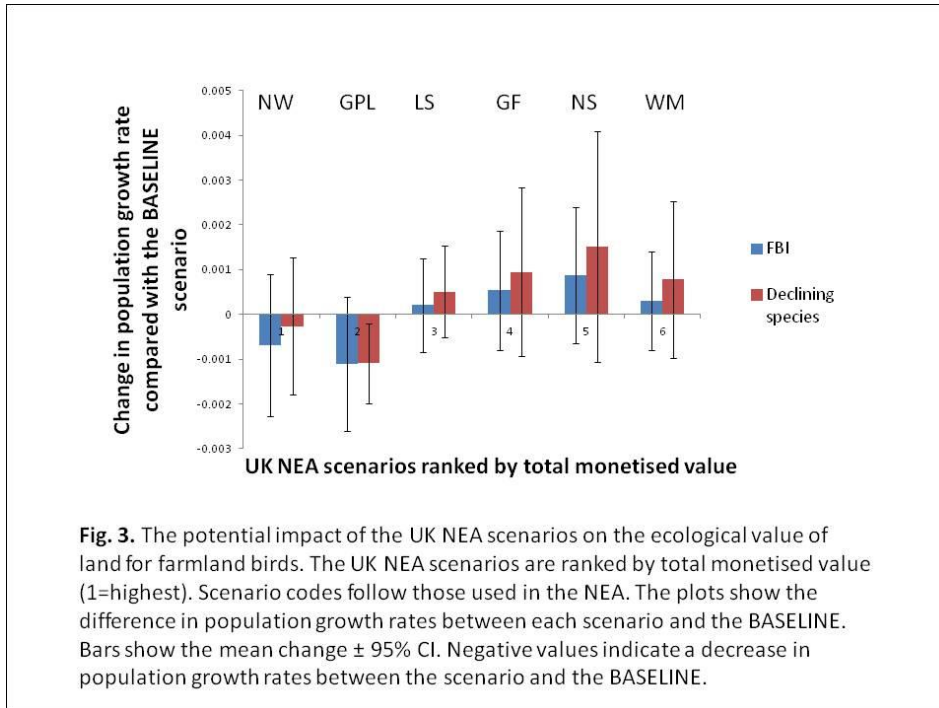

Fig. 1. The relationship between population growth rates estimated using land-use from the BASELINE scenario and observed population growth rates. Each point shows an individual species among the 19 included in the farmland bird's index.

growth rates of each species estimated by the FSMs using land-use data from the BASELINE scenario to be comparable to observed population growth rates. This is because the BASELINE scenario broadly represents contemporary land-use associated with the time period over which population growth rates were observed. We found a significant positive relationship between estimated and observed population growth rates ($R^2_{adj} = 53\%$; $F_{1,17} = 19.19$, $P = 0.00004$) (Fig. 1). The slope of this relationship is ≈ 1 ($\beta = 0.771 \pm 0.176[SE]$) and the intercept ≈ 0 ($\alpha = 0.002 \pm 0.006[SE]$), suggesting that there is so significant bias in the estimated population growth rates.

Second, in our previous work we showed that there was a significant positive relationship between the predicted number of yellowhammer days supported over-winter in a square and yellowhammer breeding population trends; whereas this relationship was weaker and non-significant for linnets (Butler *et al.*, 2010). We would expect to see similar relationships based on model predictions generated from the BASELINE land-use data, so we compared the predicted yellowhammer and linnet days supported over-winter in the BASELINE scenario with their respective breeding population trends. This comparison produced similar patterns to our previous work (Fig. 2). For yellowhammers, the relationship between bird-days and breeding population trends was positive and significant ($F_{1,450} = 5.97$, $P = 0.015$); whereas for linnets the relationship was weaker and only marginally significant ($F_{1,455} = 3.12$, $P = 0.08$).

Fig. 2. The relationship between the predicted total bird-days over-winter and breeding population trends for yellowhammer and linnets. Each point represents a 1x1 km square.

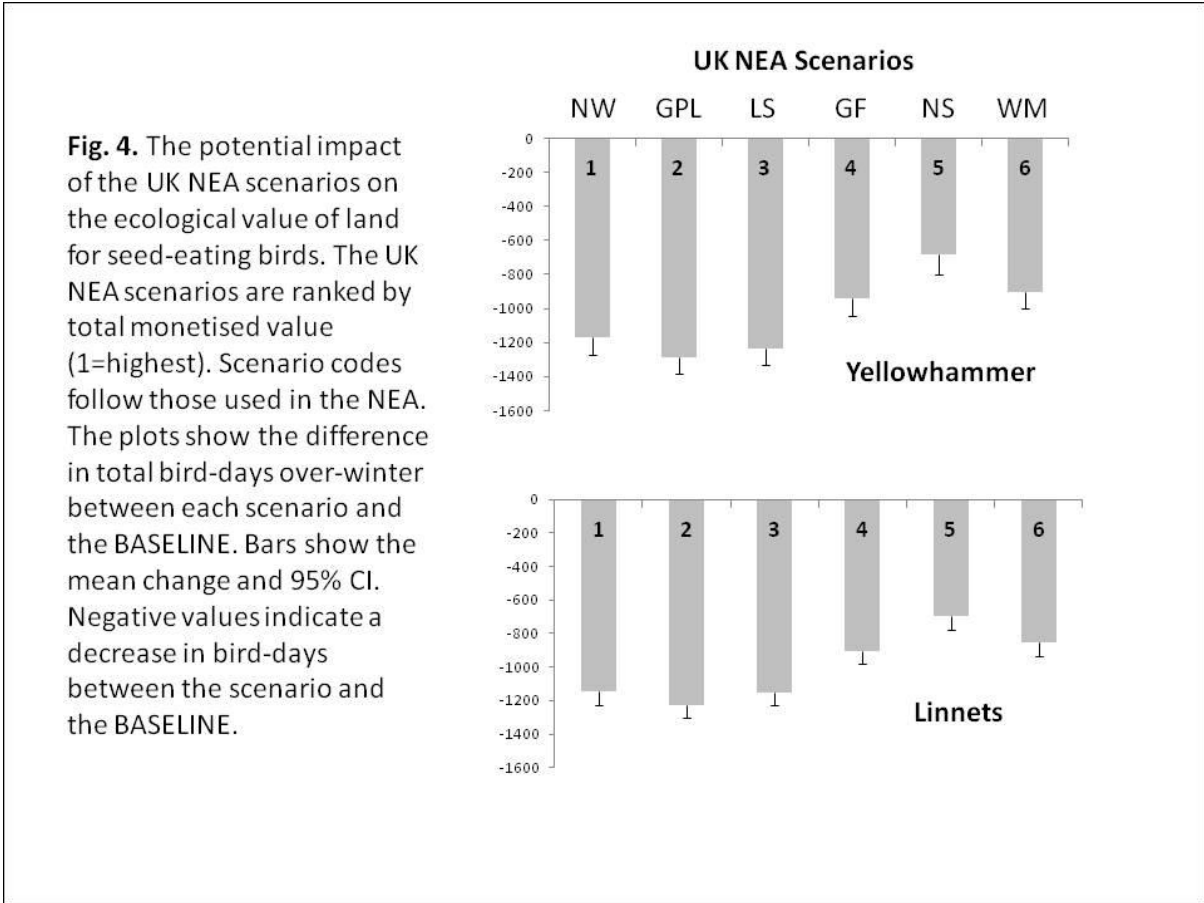*Farmland birds and ecosystem services*

To explore changes in population growth rates across the UK NEA scenarios we used two statistics. We calculated the average population growth rate across all 19 species, which is equivalent to the farmland bird index (Gregory *et al.*, 2004). This is widely used as a measure of the health of farmland bird populations. We also calculated the average population growth rate across a subset of species that had declining population trends (i.e. negative population

Fig. 3. The potential impact of the UK NEA scenarios on the ecological value of land for farmland birds. The UK NEA scenarios are ranked by total monetised value (1=highest). Scenario codes follow those used in the NEA. The plots show the difference in population growth rates between each scenario and the BASELINE. Bars show the mean change ± 95% CI. Negative values indicate a decrease in population growth rates between the scenario and the BASELINE.

growth rates) under the BASELINE scenario because these species would be of greater conservation concern than those with a stable or increasing trend. We then compared changes i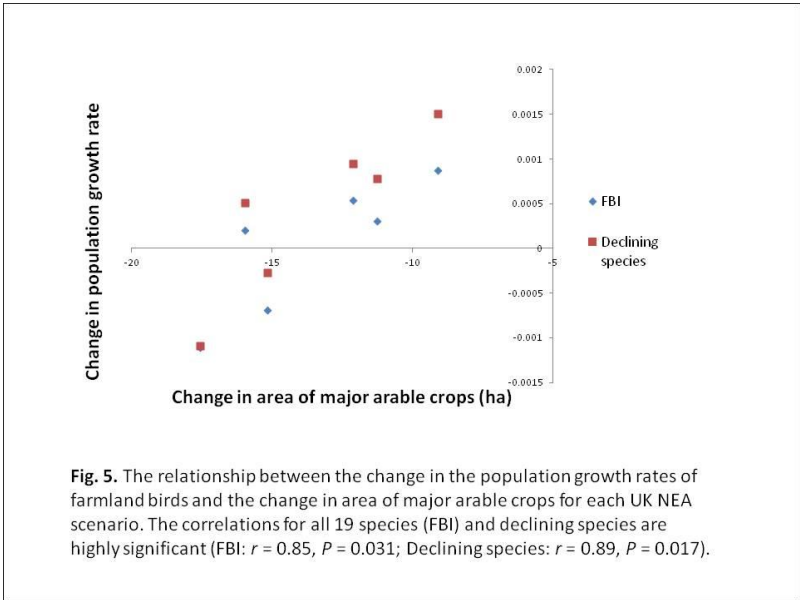n these population growth rate statistics between the BASELINE and each of the other scenarios Fig. 3. We found no evidence of co-benefits between the population growth rates of farmland birds and the overall value of ecosystem services; but some evidence of trade-offs. Overall, the impact of land-use change across the UK NEA scenarios had a rather small effect on population growth rates – the changes estimated by our FSMs are small relative to the variation in population growth rates across species (Fig. 3) (BASELINE scenario: -0.083 [turtle dove] to 0.026 [greenfinch]). The only statistically significant change was for declining species under the Green and Pleasant Land scenario, where population growth rates became significantly more negative (one-sample t-test: $t = -2.4$, $P = 0.037$)

To explore the potential impact of land-use change associated with each UK NEA scenario on seed-eating bird populations, we compared the change in yellowhammer and linnet bird-days over-winter between the BASELINE and each scenario (Fig. 4). The two bird ecotypes show comparable responses. There is a significant decline in the ecological value of lowland agricultural areas for seed-eating birds across all the UK NEA scenarios. Interestingly, this impact is greatest for the scenarios with the highest monetised values for ecosystem services (Nature@Work, Green and Pleasant Land, Local Stewardship); but lower for scenarios with the lowest monetised values (Go with the Flow, National Security, World Markets). Across scenarios, this suggests a trade-off between the ecological value of land for seed-eating birds and the values of other ecosystem services within UK lowland agricultural areas.

Fig. 4. The potential impact of the UK NEA scenarios on the ecological value of land for seed-eating birds. The UK NEA scenarios are ranked by total monetised value (1=highest). Scenario codes follow those used in the NEA. The plots show the difference in total bird-days over-winter between each scenario and the BASELINE. Bars show the mean change and 95% CI. Negative values indicate a decrease in bird-days between the scenario and the BASELINE.
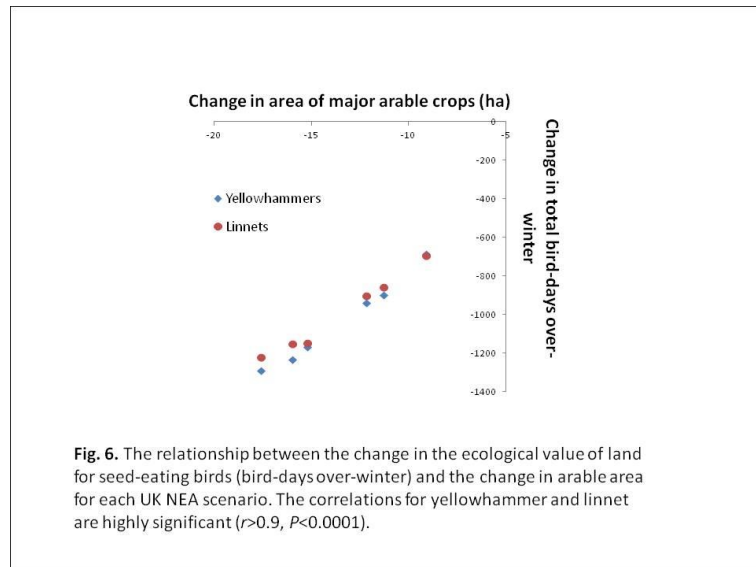
Farmland birds and land-use change

The evidence from our models suggests that land-use change associated with the scenarios that have the highest monetised value for ecosystem services have the lowest ecological value for farmland bird populations (Fig. 3, 4). These changes seem to largely reflect changes in the area of major arable crops (oil seed rape, cereals, root crops) (Fig. 5, 6). Compared with the BASELINE scenario, there is a decrease in the area of these crops across all scenarios, but this decline is greatest for those scenarios that have the highest total monetised value (i.e. Nature@Work, Green and Pleasant Land). This is because of changes in the way agricultural land is used but also because of land cover changes to non-agricultural habitats (e.g. woodlands), which are less suitable for farmland birds but important for other ecosystem services (e.g. greenhouse

Fig. 5. The relationship between the change in the population growth rates of farmland birds and the change in area of major arable crops for each UK NEA scenario. The correlations for all 19 species (FBI) and declining species are highly significant (FBI: $r = 0.85$, $P = 0.031$; Declining species: $r = 0.89$, $P = 0.017$).

emissions and recreation values). Both the changes in population growth rates (Fig. 5) and the total bird-days over-winter for seed-eating birds (Fig. 6) are strongly correlated with the changes in arable area, so the impact on farmland birds is the least for scenarios in which the decrease in the area of major arable crops is relatively small. This explains the trade-off between total monetised value and the value of land for farmland birds across the UK NEA scenarios.

Fig. 6. The relationship between the change in the ecological value of land for seed-eating birds (bird-days over-winter) and the change in arable area for each UK NEA scenario. The correlations for yellowhammer and linnet are highly significant ($r > 0.9$, $P < 0.0001$).

DISCUSSION

Functional space and mechanistic modelling

The significance of the potential impacts of land cover/use change on farmland birds reported here rests on the ecological efficacy of the models we used in the impact assessment. Our original FSMs and mechanistic model of seed-eating birds were developed with land-use data from the Breeding Bird Survey (BBS) and Winter Farmland Bird Survey (WFBS) (Butler *et al.*, 2010; Butler and Norris, 2013). Here, we have used UK NEA land-use data generated from an economic model (Fezzi and Bateman, 2011), which we have subsequently disaggregated into the land-use types recognised by our models. This required us to assume that the relative areas of different land-use types within UK NEA land-use classes remained unchanged across scenarios, and required the use of large-scale data for the disaggregation process for some squares because of discrepancies between the observed and model-generated UK NEA land-use data (see Methods). Despite the inevitable noise this process must create, performance tests of our models were good. We showed that the population growth rates for 19 species of farmland birds estimated using land-use data from the BASELINE scenario were comparable to observed population growth rates for the same species (Fig. 1). If the functional space we calculated from the BASELINE data differed significantly from functional space in contemporary lowland agricultural landscapes we would expect to see bias in the estimated population growth rates but none was found. We have shown previously that our mechanistic model of seed-eating birds accurately predicts the spatial and temporal distribution of birds (yellowhammers and linnets) between stubble (crop) types (Butler *et al.*, 2010). Furthermore, we have also previously shown that the total bird-days predicted by the model for yellowhammers is significantly, positively correlated with breeding population trends across BBS squares in lowland agricultural areas; whereas this relationship is weaker and non-significant for linnets (Butler *et al.*, 2010). This difference between the species likely reflects differences in drivers of population decline – changes in

survival possibly associated with the loss of seed-rich habitats is considered the major driver of population decline in yellowhammers; whereas changes in productivity are considered important in linnets (Siriwardena *et al.*, 2000). Here, we show that the predicted total bird-days for yellowhammers and linnets generated from the BASELINE scenario produced comparable relationships with breeding population trends to our previous work (Fig. 2). We conclude, therefore, that the performance of both our FSMs and mechanistic models using observed and UK NEA land-use data is sufficiently comparable to justify exploring predictions based on land-use change associated with the other UK NEA scenarios.

Farmland birds and ecosystem services

Our analysis found no evidence of co-benefits between farmland biodiversity and the value of ecosystem services across the UK NEA scenarios; but some evidence for trade-offs. The ecological value for farmland birds was lowest for the scenarios that had the highest total monetised value for ecosystem services (i.e. Nature@Work, Green and Pleasant Land) (Fig. 3, 4). We found rather small changes in the population growth rates of farmland birds across the NEA scenarios, but we did document a significant deterioration in the population growth rates of species of conservation concern under the Green and Pleasant land scenario. We found stronger but comparable patterns for seed-eating birds. The health of farmland bird populations is widely used as a measure of the conservation value of farmland and hence the sustainability of farming practices (Gregory *et al.*, 2004; Gregory and van Strien, 2010). Furthermore, significant public funds are invested in agri-environment schemes that are designed to improve the biodiversity value of farmland in general (Kleijn *et al.*, 2011), and halt and reverse population declines among UK farmland birds in particular (Vickery *et al.*, 2004; Davey *et al.*, 2010; Baker *et al.*, 2012). Our results suggest that scenarios associated with significant improvements in the value of ecosystem services are not well aligned with these conservation priorities in UK lowland agricultural landscapes. In general terms, biodiversity conservation may not be a simple by-product of improved policies and practices that protect the values of other ecosystem services, at least in the context of farmland birds in UK lowland agricultural landscapes.

Why does this trade-off exist? Changes in land-use and land cover associated with the NEA scenarios with the highest monetised value for ecosystem services results in the loss of important agricultural habitats for farmland birds (Fig. 5, 6). Major arable crops provide key nesting and foraging resources for a range of farmland bird species, particularly when spring-sown crops form part of the rotation system (Gillings *et al.*, 2005; Baker *et al.*, 2012). The loss of these resources drives the changes in farmland bird populations described by our models. The loss of arable habitats is caused by changes in land cover, particularly an increase in the area of woodland. These changes result in major benefits to ecosystem services – they reduce greenhouse gas emissions and increase recreational values significantly (Bateman *et al.*, 2013) (Table 1). Of course, these land cover changes may have biodiversity benefits, particularly for woodland species, which are not assessed by our analysis. Nevertheless, the key point is that land cover/use changes that benefit ecosystem

services the most have a detrimental impact on the conservation value of farmland across the UK NEA scenarios.

Table 1. Changes in ecosystem services across the UK NEA scenarios based on the sample 1x1 km lowland agricultural squares used in our farmland bird modelling. The cells of the table show the mean change in ecosystem service values compared with the BASELINE scenario. Negative values mean they have decreased compared with the BASELINE. Figures in parentheses are the 95% confidence limits. $***P < 0.001$, $*P<0.05$.

UK NEA Scenario	Ecosystem Services[1]		
	Greenhouse Gas Emissions (tonnes of CO_2 equivalents/ha)	**Farm Gross Margins** (£/ha)	**Recreation** (Visitors/ha)
GPL	-0.2*** (-0.21, -0.19)	-3.97*** (-5.72, -2.23)	381.2*** (351.2, 411.3)
GF	0.006* (0.003, 0.011)	9.07*** (6.3, 11.84)	225.3*** (206.7, 244)
NS	-0.07*** (-0.08, -0.06)	17.75*** (14.36, 21.13)	233.3*** (216, 250.5)
NW	-0.29*** (-0.3, -0.28)	-5.82*** (-8.09, -3.55)	795.2*** (736, 854.3)
LS	-0.02*** (-0.028, -0.013)	11.13*** (8.97, 13.29)	192.3*** (170, 215)
WM	0.03*** (0.023, 0.036)	10.94*** (7.75, 14.13)	-2.4 (-11.7, 6.8)

[1]Data from Bateman et al. (Bateman *et al.*, 2013)

One option for dealing with this type of trade-off in terms of land-use planning would be to consider minimizing the impact of land-use change on conservation values as a constraint (Bateman *et al.*, 2013). For example, in lowland agricultural landscapes the Local Stewardship scenario has a minimal impact on population growth rates across farmland bird species (Fig. 3), a negative impact on the provision of arable habitats for seed-eating birds (Fig. 4), but positive impacts on ecosystem services and farm gross margins (Table 1). If agri-environmental management could be deployed to reduce the impacts on seed-eating birds, then the land-use changes under the Local Stewardship scenario would improve the profitability of farms and increase the value of ecosystem services; whilst minimizing any adverse impacts on farmland biodiversity. This shows that linking biodiversity modelling with the spatial analysis of ecosystem services can provide a powerful framework for identifying and addressing potential conflicts caused by land-use change.

In summary, our results suggest that outcomes for ecosystem services and biodiversity will depend critically on the specific impacts of the land cover/use changes involved. An ecosystems approach enables biodiversity values to be considered alongside the values of other ecosystem services in decision-making (Bateman *et al.*, 2013).

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